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SOME NEW ASPECTS OF THE FERN PLATYZOMA MICROPHYLLUM

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Since this north Australian fern was described by Robert Brown in 1810 and placed in the *Gleicheniaceae*, it has been the subject of several papers. Because of its unusual stelar structure and absence of leaf gaps it was considered particularly in theories relating to the origin of the stele. In the most recent of these morphological studies by J. M. Thompson (1919) the literature is reviewed. F. O. Bower (1926) in his survey of the primitive ferns cites Thompson's work and figures the reconstruction of the stele and the irregularities of the sporangium. In connection with his studies on the *Gleicheniaceae*, R. E. Holttum (1956) has discussed the relationships of *Platyzoma*. He excludes it from that family on the basis of the filiform leaves, the occurrence of waxy indument and the terminal position and characters of the sporangium. He tentatively refers it to a place among the gymnogrammoid ferns on evidence drawn from a comparison with *Jamesonia*. While there are good reasons for excluding *Platyzoma* from the *Gleicheniaceae*, there are some objections to its close alliance with *Jamesonia*. A study of *Platyzoma* was undertaken in search of new evidence which might help to establish its relations more certainly. Observations have been made on the following specimens in the Gray Herbarium and the United States National Herbarium[1].

[1]I am most grateful for the loan of specimens from the United States National Herbarium, and for the opportunity to study the collections and the use of facilities at the Gray Herbarium.

AUSTRALIA. QUEENSLAND: near Hughenden, *Brass & White 64* (fragment GH ex K); northern Queensland, *Hann* (US); Thursday Island, *N. J. Hey*, in 1917 (US); Dimbulah, Cook District, *Hubbard & Winders 6856* (US); Hughenden, Burke District, *Hubbard & Winders 7592* (US); Rockingham Bay, *F. Müller* (GH); between Inglewood and Millmerran, Darling Downs, *C. T. White 9705* (GH); between Cecil Plains and Millmerran, Darling Downs, *White & Webb 1177* (GH). NORTHERN TERRITORY: east of Borroloola, *R. A. Perry 1851* (US); east of Carlton Station, *R. A. Perry 3005* (US); in Gulf of Carpentaria, Groote Eylandt, *R. L. Specht 197* (US); Port Bradshaw, Arnhem Land, *R. L. Specht 716* (US); Oenpelli, Arnhem Land, *R. L. Specht 1252* (US). WESTERN AUSTRALIA: Cambridge Gulf, *F. Müller*, (GH); east of Kimberly Research Station, *R. A. Perry 2566* (US).

Observations on Platyzoma microphyllum

Roots. — The roots are long, coarse and of a diameter nearly equal to that of the petioles. They arise from the lower surface of the rhizome. The outer tissue of the roots appears spongy and consists of large, lustrous, light brown, parenchyma cells. Long persistent root hairs arise from the surface of these cells forming dense mats in which particles of white sand may be enmeshed.

Rhizome. — The rhizome is dorsiventral, ca. 0.4 cm. in diameter with a tomentum of rigid, concolorous, lustrous, rust colored, multicellular trichomes. The trichomes are relatively long and consist of about 30 - 60 cells (Fig. 1). These cells are as long as or up to four times longer than broad, and are not arranged in any regular sequence of size. The base of the trichome may be catenate (Fig. 2); the cells being flattened and twisted. The terminal cell is short and bulbous. The leaves are close but irregularly placed on the rhizome or fasciculate. Many arise from the upper and lateral surfaces but some of the pinnate leaves and most of the filiform ones arise from the lower surface of the rhizome. The longest rhizome (with attached leaves) was 4 cm. long and there were 4 circinate leaves at the apex, 34 pinnate leaves and about 50 filiform leaves. The filiform leaves in some specimens are fascicled while in others they are quite uniformly distributed along the entire rhizome. Details of the structure of the rhizome are given by Thompson (1916). It is described as a medullated protostele with

a discontinuous inner endodermis and lacking leaf gaps.

Pinnate leaves. — Fully developed leaves have an expanded apex with a terminal pinna although many leaves are not entirely developed. In the smallest complete leaf the petiole was 2.5 cm. long, the lamina 11.0 cm. long and 0.3 cm. wide. The lamina of the longest leaf, with a broken apex, was 32.0 cm. long, 0.4 cm. wide and the petiole was 8.0 cm. long. Most leaves are about 24.0 cm. long.

PETIOLE: The petiole is terete or oval near the rhizome, atro-purpureous and with sparse, multicellular, capitate trichomes similar to those of the rhizome. At the apex of the petiole the adaxial half is flattened in three planes and the abaxial half is convex. There are no stomata on the petiole but small mounds of sclerotic tissue rarely occur.

RACHIS: The adaxial surface of the rachis is flat, slightly lighter in color than the petiole or sometimes greenish. The lateral surfaces, on which the pinnae are borne, are flat or slightly grooved. There are abundant, glandular, multicellular trichomes on the lateral and adaxial surfaces of the rachis (Fig. 3). The apical portion of the rachis is attenuate and heavily indumented.

PINNAE: The lamina is once pinnate with about 500 small, simple pinnae which are easily detached from the rachis in dried specimens. Articulation occurs in the stalk without specialized tissue. Most leaves are wholly sterile. Fertile pinnae occur in zones usually in the terminal half or quarter of the lamina and on one or both sides of the rachis. One leaf consisted of 433 pinnae of which 11, borne on one side of the rachis, were fertile. The pinnae are somewhat bladder-shaped with a central slit. The margins are more or less enrolled and nearly meet at the center of the pinna. The pinna *stalk* is usually brown, 0.1 - 0.25 mm. long, 0.2 mm. broad with a cushion of parenchyma cells at the apex which is attached to the lower epidermis and is very glandular. The cells of the *lower epidermis* are thin walled and about 4 to 6 times longer than broad (Fig. 4). In surface view the cell walls are undulate with rounded lobes. Stomata occur only on this surface and are abundant adjacent to the

costa and more diffuse towards the margins. Two- or three-celled, capitate glands (Fig. 5) which secrete copious quantities of yellow wax-like substance, are especially abundant along the veins. The mesophyll is thick and with many large lacunae. The cells of the *upper epidermis* are thick walled and have a shape and a pattern distinct from those of the lower epidermis (Fig. 6). The pattern, which can be observed in dried specimens under 15 × magnifications, consists of a band of elongate cells about 6 to 12 times longer than broad with undulating walls. This band extends through the center of the pinna from the stalk to the apex where it becomes flabellate. Adjacent to it and along the curved sides of the pinna the cells are broader and deeply dissected. The *vascular system* of the pinna is a short sympodium with 6 - 12 lateral branches (Fig. 7). The central vein is slightly flexuous and terminates in an unequal dichotomy. The lateral veins are unbranched and become broader toward their distal end. They terminate well back of the pinna margin and the ends are acute or slightly enlarged. The veins are situated in the spongy mesophyll somewhat closer to the upper than the lower epidermis. They consist of a cord of short, thick-walled tracheids so tightly joined that the entire sympodium can be withdrawn from a pinna softened in sodium hydroxide.

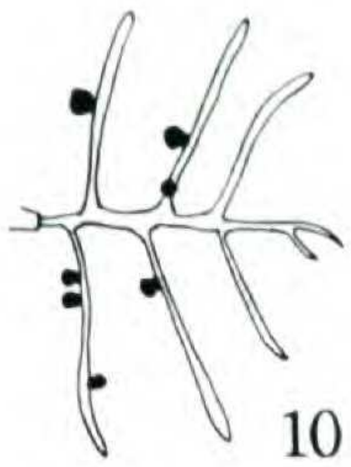
STERILE PINNAE: These are rigid herbaceous, 0.5 - 4.0 mm. long, 0.5 - 2.0 mm. wide, ovate or somewhat orbicular with enrolled margins (Fig. 7). A central slit extends from the stalk to short of the apex and the pinna margins adjoining this are strongly papillate. There are some *unusual pinnae* on the leaves of one collection (*Hubbard & Winders 6856*). The lower pinnae on these are 2 or 3 times as long as the normal ones and clavate or boat-shaped (Fig. 8). The base is narrowed and decurrent on the broad and greenish adaxial surface or on the light brown colored lateral surface of the rachis. If a pinna stalk can be distinguished from the decurrent tissue, it is longer and broader than those of the normal pinnae and only partially brown. The margin is irregular with protruding, elongate cells. The pinna is

thickened on its abaxial surface by a ridge of tissue extending from the stalk to the apex. Such a ridge also occurs in otherwise normal pinnae of the lamina and there seem to be transitional forms between these elongate ones and the normal pinnae.

FERTILE PINNAE: These are slightly larger than the sterile pinnae, orbicular and the margins are not or only slightly enrolled. The papillae from opposite margins may be somewhat enmeshed and close the bladder-shaped pinnae. The fertile pinnae are often a darker brown color and more wrinkled than the sterile pinnae.

Filiform leaves. — These are simple, linear structures with attenuate apices. The apical portion is straw colored or light brown, the basal portion is atropurpureous. They are 3.0 - 8.0 cm. long, 0.05 cm. wide. There are two prominent grooves, presumably on the adaxial side, and two or more shallow ones on the other side extending nearly the length of the leaves. Stomata may be more or less in rows in the shallow grooves (Fig. 9).

Sporangia. — Sporangia are attached along the lateral veins usually nearer to the costa than to the distal end of the vein (Fig. 10). They have been observed on the distal portion of the vein but not in a terminal position. There is considerable variation in the size of the sporangia for among mature ones within the same pinna some may be twice the size of others. There is also variation in the shape, spore content and the position and structure of the annulus. Such irregularities are discussed and illustrated by Thompson (1917, p. 160) and Bower (1926, p. 209). There is however a rather uniform sporangial type which will be described here. Sporangia in several stages of development are found along a single vein and up to 13 have been observed on a single pinna. The sporangium stalk is short, usually of two or three tiers of cells. Three basal cells have been observed in immature sporangia. At the capsular end of the stalk there are either 3 or 4 cells which differ from other stalk cells in having striated thickenings. The capsule of the sporangium is spherical, the annulus is broad, slightly raised



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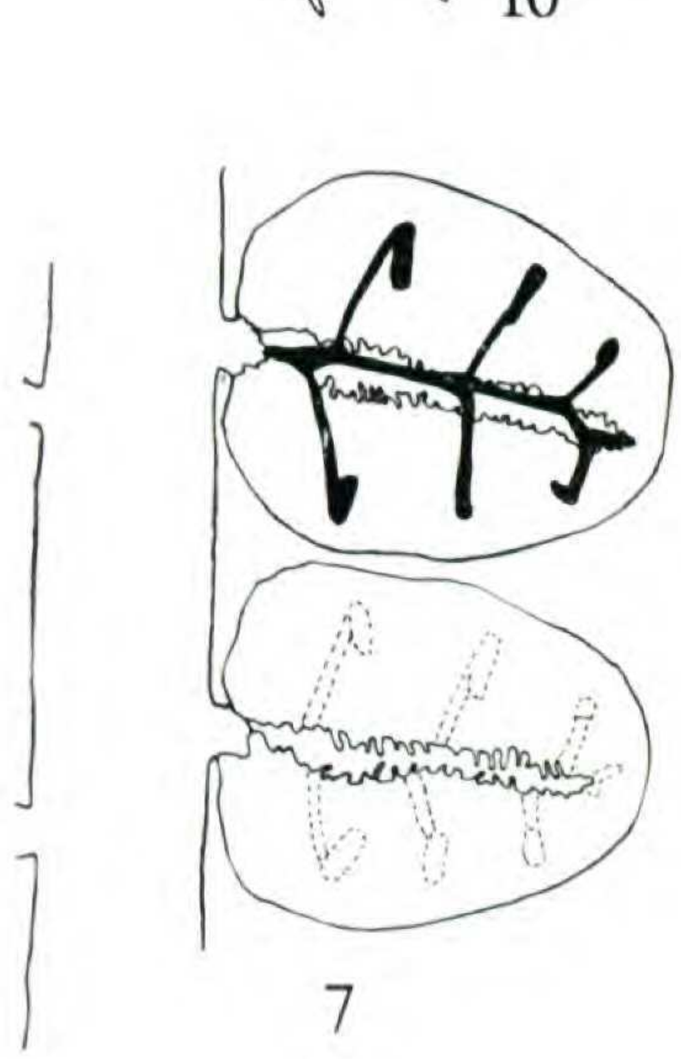

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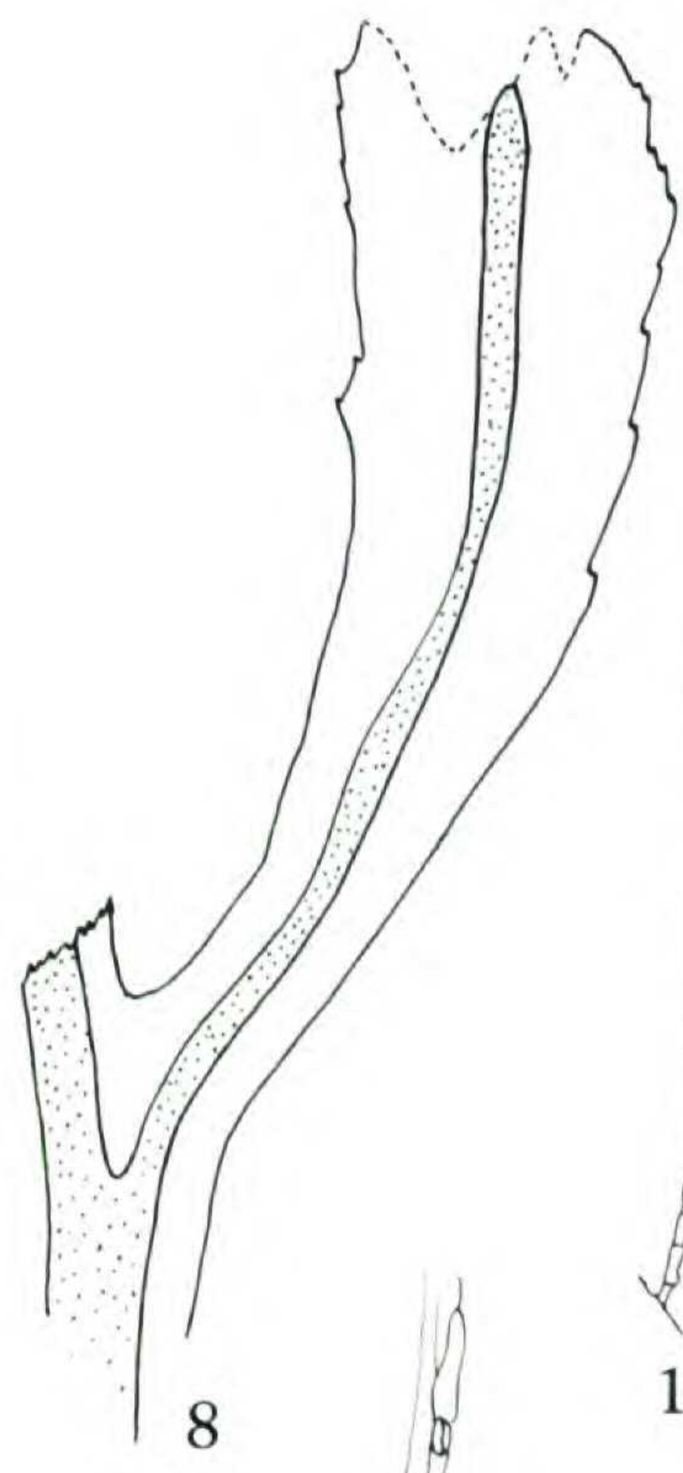

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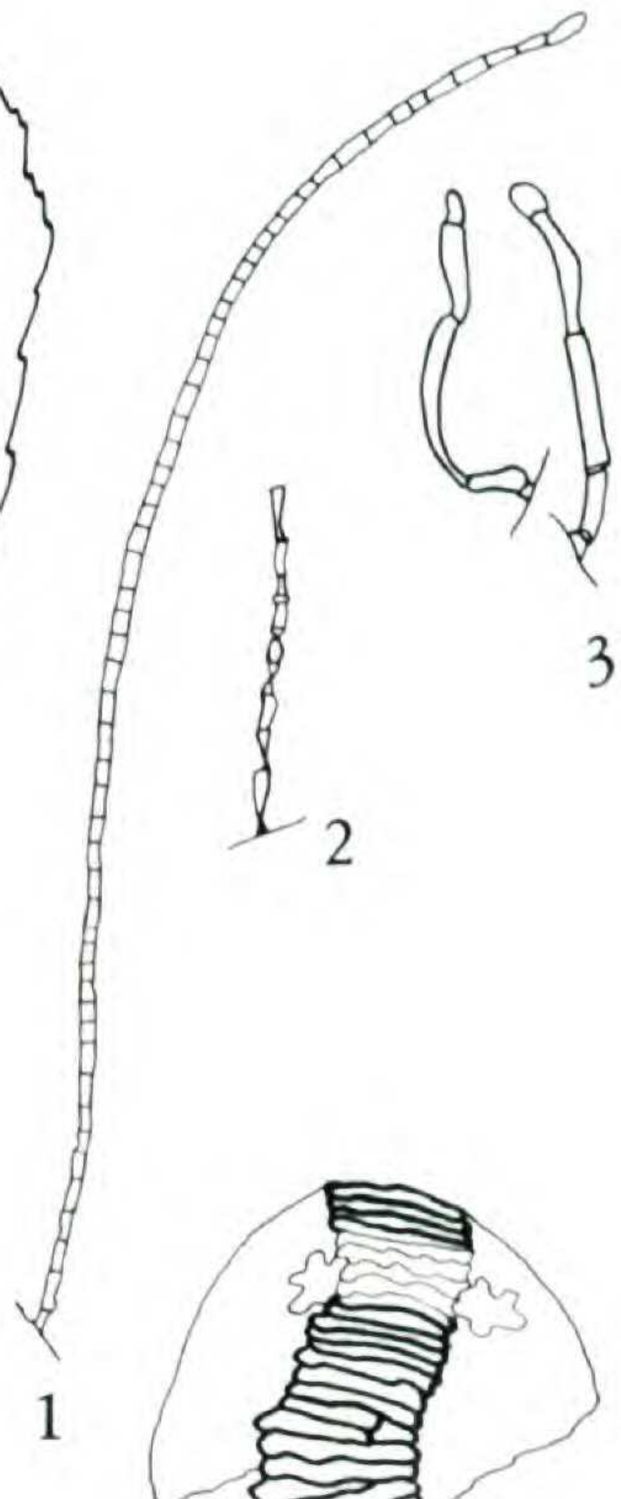

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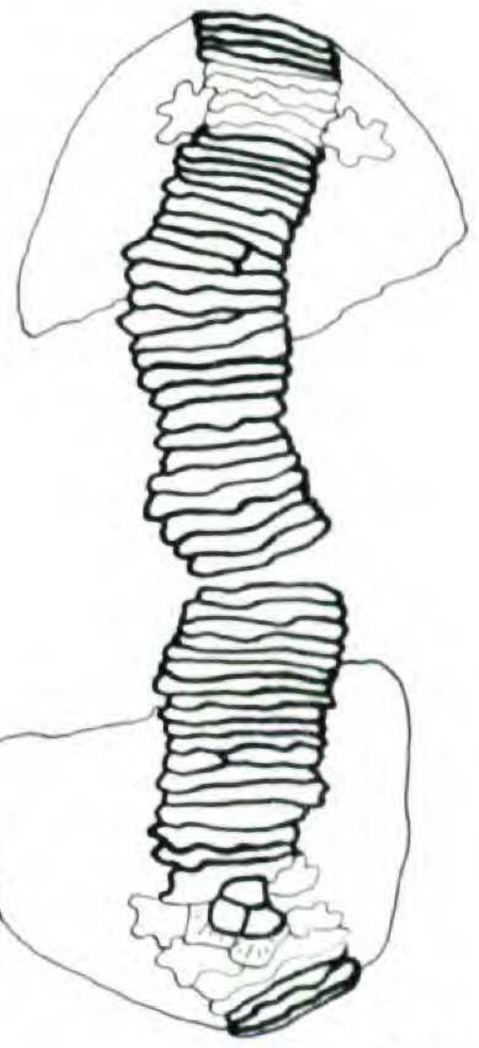

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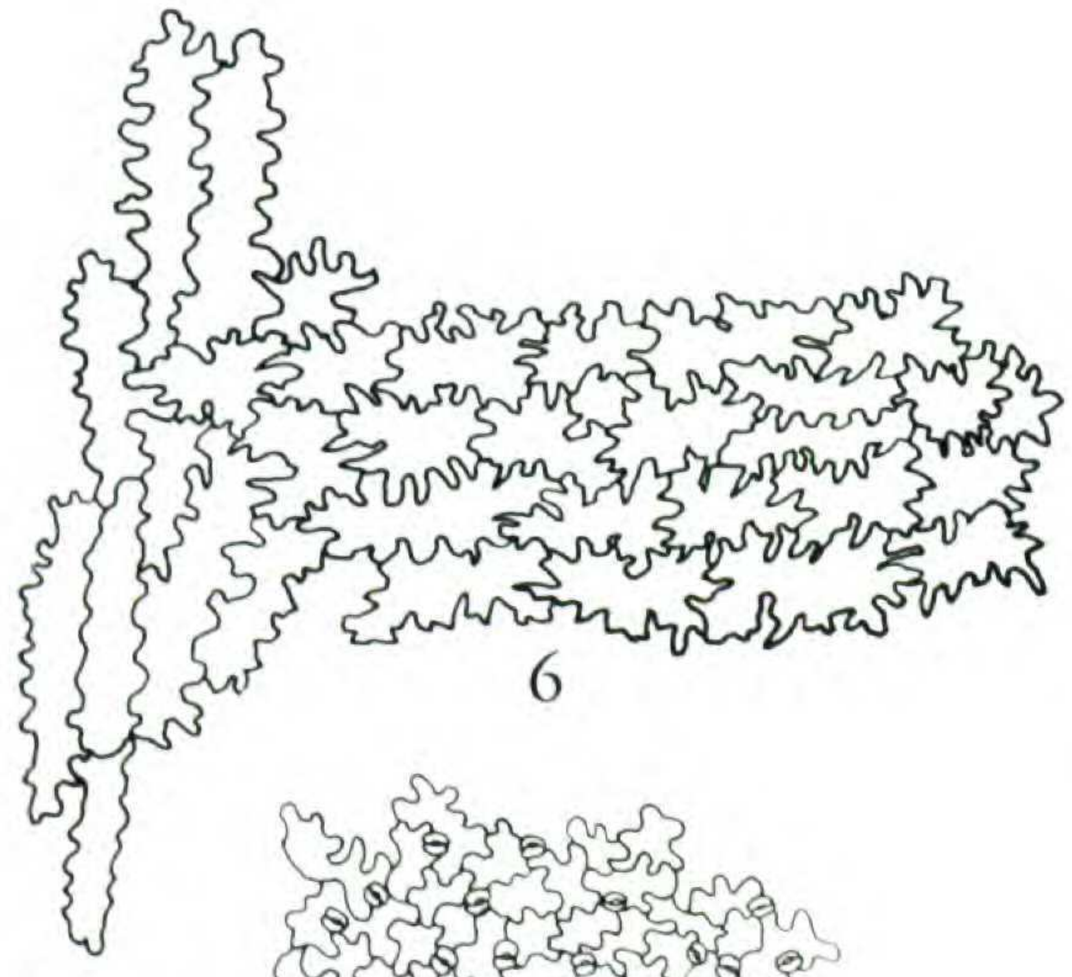

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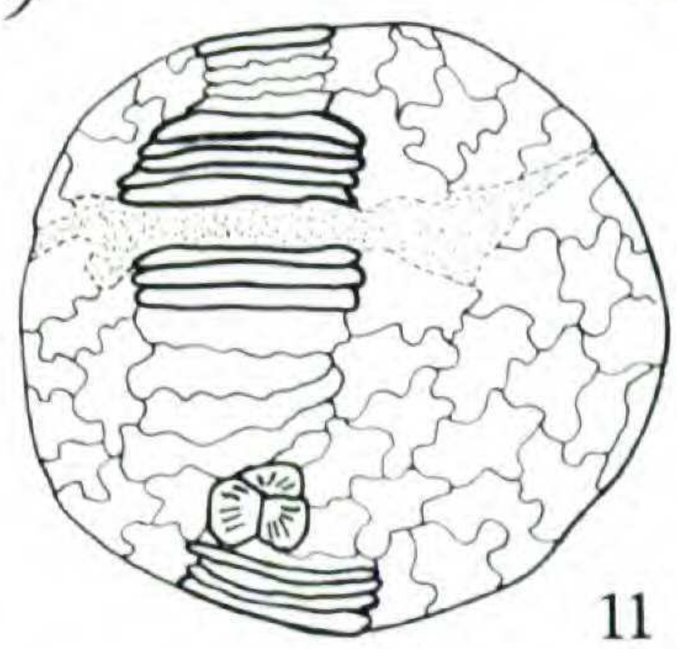

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Platyzoma microphyllum

and usually more or less oblique with the capsule faces correspondingly unequal in size (Fig. 11). The annulus (Fig. 12) is composed of a single row of cells which may vary in size and shape, but its width is roughly one third the diameter of the capsule. There are about 40 indurated cells which extend from the base of the capsule around and below its apex. There are about 4 cells with thin and undulating walls which interrupt this annular series. These are followed by 7 - 14 indurated cells similar to those of the annulus. The sporangium opens between these indurated cells at a point usually above their center. There are a few, usually 2 or 4, cells with thin and undulating walls between these indurated ones and the sporangium stalk. The annulus is interrupted by the stalk and the rupture of the sporangium occurs between several indurated cells which resemble those of the longer annular series. A unique characteristic of the sporangium is the cells of the capsule faces (Fig. 11). In surface view these are strongly undulating and somewhat resemble the cells of the lower epidermis.

Spores. — The number of spores in a sporangium and their size seem to correlate with the size of the sporangium. The larger sporangia usually contain 16 large spores and small sporangia contain 32 small spores. There are also sporangia intermediate in size and in one of these, which was open, I found a single large spore nearly filling the capsule and 4 small spores. In six collections examined both 16- and 32-spored sporangia were found on the same pinna. Most

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Tracings from cleared material of *Platyzoma microphyllum* — FIG. 1. Rhizome trichome, × 10, *Perry 2566*. FIG. 2. Catenate base from rhizome trichome, × 15, *Perry 2566*. FIG. 3. Glandular trichomes from rachis, × 35, *White 9705*. FIG. 4. Portion of lower epidermis of pinna, × 45, *Specht 1252*. FIG. 5. Glands from abaxial surface of pinna, × 60, *Specht 197*. FIG. 6. Portion of the upper epidermis of the pinna. Elongated cells at the left are from the central band, × 45, *Specht 1252*. FIG. 7. Sterile pinnae on a portion of the rachis. The venation darkened in the upper; the lower showing the outline of the margins, the veins in broken lines, × 15, *White 9705*. FIG. 8. An elongate pinna, decurrent on a portion of the rachis, the apex torn by flattening, the vascular tissue shaded, × 15, *Hubbard & Winders 8656*. FIG. 9. Portion of the epidermis of a filiform leaf with stomata, × 45, *Specht 1252*. FIG. 10. Vascular system of a pinna with attached immature sporangia, × 15, *Brass & White 64*. FIG. 11. A sporangium with the aperture shaded. With indurated cells above and below the gap, the three celled stalk in the lower part, × 70, *Brass & White 64*. FIG. 12. An opened annulus of a sporangium, with a three celled stalk in the lower part, × 70, *Brass & White 64*.

spores are tetrahedral with a trilete proximal face. In a few sporangia there were also bilateral spores some of which were trilete with ridges of unequal length and others were monolete. The spores are prominently sculptured. The proximal face has long, broad ridges which are somewhat parallel to the commissural ridges and are connected by shorter ones to form a reticulum. The distal face is also prominently sculptured but the rugae are mostly short and form circular or irregular loops. In the equatorial region there may be one or a few parallel ridges nearly continuous around the spore. The spores are often retained in open sporangia. They are also found free within the pinna, sometimes covered with the yellow indument from the glands.

Discussion

Some of these observations are at variance with those previously reported by Thompson and Holttum. The first is the position of the sporangia which Thompson (1916) reports as terminal on the vein ends. Although sporangia may occur on the distal portion of the veins, I have not observed them to be exactly terminal in cleared pinnae. They occur on the lateral veins adjacent to the costa and along the veins to near the distal end. The position is best observed when the sporangia are immature. I interpret them as lateral rather than terminal on the veins. The apical growth of the leaves has been described as indefinite. Some leaves have undeveloped apices which may expand slowly; however they do terminate in a completely developed apex before the lower pinnae have deteriorated. The leaves are determinate and the lamina is imparipinnate. The spores are mostly tetrahedral and trilete as reported but a few spores have been observed which are bilateral and monolete.

From this survey of *Platyzoma* it was noted that there are certain similarities with the *Schizaeaceae*. A medullated protostele with sclerosed pith and inner endodermis are reported by Bower (1926) in species of *Anemia* and *Schizaea*. The rhizome in these genera has multicellular trichomes. Reduced filiform leaves with a central vascular trace and stomata are found in several species of *Schizaea* — *S. fistu-*

losa Labill., *S. papuana* Brause, and they are especially abundant in the North American *S. pusilla* Pursh. In the filiform leaves of *Platyzoma* the guard cells may be larger relative to the adjacent cells than in *Schizaea*, but the form of the intra-stomatal cells is similar. In the elongate pinnae which were found in one collection of *Platyzoma* there is a resemblance to the form of the lobes of the lamina in *Schizaea*. Since these pinnae have been found in only one specimen of *Platyzoma* they might be considered as abnormal. In the company of other similarities with *Schizaea*, I am inclined to regard them as something more than an anomalous condition. On the leaves of many species of *Anemia* and *Schizaea* there are 2- or 3-celled capitate glands. These are similar to the glands on the pinnae of *Platyzoma* although the basal cell may be larger and there is no yellowish indument. The sporangium of *Platyzoma* is most remarkable in its spherical shape, short stalk, its broad, more or less oblique annulus which is scarcely raised from the surface of the capsule, and especially in the undulating cell walls of the capsule faces. In *Mohria* and some species of *Anemia* the sporangia are spherical and short stalked or sessile. The cell walls of the capsule in *Schizaea melanesica* Sell. and *S. confusa* Sell. (Selling 1944b, 1947) are undulating and similar to those of *Platyzoma*. There is also similarity in the reticulate sculpture of the spores between *S. confusa* and *Platyzoma*. In his studies on the spores of *Schizaea* O. H. Selling (1944a) reports variations in size and sculpturing. In *S. fistulosa* there seem to be two sizes which show some correlation with the geographic distribution. It would be of interest to determine whether such variation in spore size in *Schizaea* and *Platyzoma* might be related to the apogamous condition as it is in species of *Pellaea* (Tryon & Britton, 1958).

In addition to an evaluation of similarities between *Platyzoma* and *Schizaea*, the distinctive character of the *Schizaeaceae* — the apical annulus — must be considered, and also the possibility of parallel reduction in these two genera. Resemblances in the sporangia are remarkable and

there is little possibility of parallel reduction in this structure. In *Platyzoma* the annulus is usually oblique — with unequal capsule faces, it is scarcely raised from the surface and is about one third the diameter of the capsule. There is a series of indurated cells in the stomial region and epidermal-like cells in the capsule faces. In these features the resemblance seems to be with *Schizaea* although there are similarities with species of *Anemia* and *Mohria* which have spherical sporangia, and in which there are several non-indurated cells in the apical portion of the sporangia. While the sporangia of *Platyzoma* are not identical to those of the *Schizaeaceae*, in this structure and in some aspects of the leaves there are resemblances closer to that group than to any other family.

There is also similarity to the *Polypodiaceae* particularly in the interruption of the annulus by the sporangium stalk. *Platyzoma* can be placed here in the subfamily *Gymnogrammoideae* and in the tribe *Gymnogrammeae* on the superficial sporangia following the course of the veins. In this tribe it would be allied to *Eriosorus* and *Jamesonia* by its monomorphic leaves and pubescent rhizome. It was tentatively placed here by Holttum (1956).

In the course of the preparation of a revision of *Jamesonia*, I have studied its species in some detail and wish to remark upon a number of characters of *Jamesonia* which differ from *Platyzoma*. The species of *Jamesonia* grow mainly on the South American páramos at altitudes from 2350 to 5000 meters. The species center in Colombia and Venezuela and occur northward into southern Mexico and southward to Bolivia and eastern Brazil. In the páramos *Jamesonia* is usually found growing in the shelter of rocks with grass or moss. The rhizomes are horizontal, creeping, dichotomously branched, with spirally arranged leaves, and are sparsely to densely covered with simple, multicellular trichomes. In some species the trichomes have more massive bases and become rather scale-like. The leaves in some but not all species are indeterminate and there are no reduced

or filiform leaves such as in *Platyzoma*. Young leaves are produced behind the apex on older parts of the rhizome and it is possible that these or a cluster of old petioles may have been the basis of the report of reduced leaves. A dense pubescence or glutinous exudate is characteristic of the leaves of *Jamesonia* but ceraceous indument is rare. It is indeed of such rare occurrence on the abaxial surface of the pinnae that it has been observed there in only one collection — the type of *J. ceracea* Maxon. It is perhaps in the form of the pinnae that *Jamesonia* and *Platyzoma* differ most markedly. The pinnae in *Jamesonia* are generally flat with the margins more or less enrolled. The margin is usually membranous or ciliate. The pinnae are relatively long stalked, rarely subsessile and in two species adnate. The venation of the pinnae is dichotomous with the ramifications branching and terminating usually in numerous ultimate veins which extend to or near the pinna margin. The form of the annulus may be somewhat irregular but there are generally about 20 raised and indurated cells. There is a distinct stomial region with 2 - 4 indurated lip cells which are smaller than those of the annulus. The sporangial stalk may be short — one quarter or less than the length of the capsule or equal to it in length. The spores of *Jamesonia* are entirely different from those of *Platyzoma* in the type of sculpture. They are trilete with 3 broad smooth or verrucate planes on the proximal face; there is a prominent equatorial ridge or wing and 3 broad ridges forming a triangle on the distal face. *Jamesonia* is a specialized group, closely related and with species transitional to *Eriosorus*. Although there is some resemblance between *Jamesonia* and *Platyzoma* the relationship is not a close one.

Platyzoma is properly excluded from the *Gleicheniaceae* and can, in the present classification, be placed in the *Polypodiaceae*. This disposition however, adds to the problems of the definition of that family. There is general agreement that the *Polypodiaceae*, as treated by Christensen, is polyphyletic but there is no clear understanding of the natural groups.

It is my belief that the *Schizaeaceae* is a source from which some of those groups have been independently derived. *Sinopteris* and some species of *Cheilanthes* have similarities with *Mohria; Eriosorus, Jamesonia* and *Pterozonium* comprise a group having certain resemblances to *Anemia.* While in *Platyzoma* there are similarities with *Schizaea* in the shape of the pinnae and lobes of the lamina, the filiform leaves, the spores and particularly in the structure of the sporangium.

LITERATURE CITED

Bower, F. O. 1926. The Ferns. Vol. II. The Eusporangiate and Other Relatively Primitive Ferns. 344 pp. University Press. Cambridge, England.

Brown, Robert. 1810. Prodromus Florae Novae-Hollandiae et Insulae Van Diemen. J. Johnson. London, England.

Christensen, Carl. 1938. Filicinae. In Verdoorn's Manual of Pteridology. The Hague, Netherlands.

Holttum, E. R. 1956. On the nature and possible relationships of the fern genus *Platyzoma* R. Br. Kew Bull. No. 3: 251-253.

Selling, O. H. 1944a. Studies in the recent and fossil species of *Schizaea,* with particular reference to their spore characters. Meddel. Göteborgs Bot. Träd. **16**: 1-112.

———————1944b. A new species of *Schizaea* from Melanesia and some connected problems. Svensk Bot. Tidskr. **38**: 207-225.

———————1947. Further studies in *Schizaea.* Svensk Bot. Tidskr. **41**: 431-450.

Thompson, J. M. 1916. The anatomy and affinity of *Platyzoma microphyllum* R. Br. Trans. Roy. Soc. Edin. **51**: 631-656.

———————1917. A further contribution to the knowledge of *Platyzoma microphyllum* R. Br. Trans. Roy. Soc. Edinb. 52: 157-165.

———————1919. The morphology of the stele of *Platyzoma microphyllum,* R. Br. Trans. Roy. Soc. Edinb. **52**: 571-595.

Tryon, A. F. and D. M. Britton. 1958. Cytotaxonomic studies on the fern genus *Pellaea.* Evolution **12**: 137-145.